SHORT COMMUNICATION

Ant mimicry in the spider *Myrmecotypus iguazu* (Araneae: Corinnidae), with notes about myrmecomorphy in spiders

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Abstract.   We describe the mimetic relationship between the ant-like spider *Myrmecotypus iguazu* Rubio & Arbino 2009 (Araneae: Corinnidae) and the carpenter ant *Camponotus sericeiventris* Guérin (Hymenoptera: Formicidae), studied in a subtropical rainforest in Iguazú National Park, Argentina. The morphological adaptations, aspects of coloration, and behavior responsible for the ant-like appearance in *M. iguazu* (the mimic) provide strong evidence that its model is *C. sericeiventris*. Both field observations and field and laboratory experiments suggest that this spider is a Batesian mimic.

Keywords: Ant-like spider, Batesian mimics, behavior, mimetic relationship, Paranaense rainforest

Spiders are generalist predators found in diverse environments. Because most of them are small, soft-bodied arthropods and lack defensive protection against larger predators, they can become prey of these predators, especially of those that use their vision to detect prey (such as wasps, birds, spiders, frogs, and small lizards). Many species of spiders have evolved adaptations that are thought to provide protection against such visually hunting predators.

Many spiders, particularly in the families Salticidae and Corinnidae, have evolved mimetic resemblance to ants, or myrmecomorphy (Simon 1897; Mello-Leitão 1939; Galiano 1965, 1966, 1967, 1969; Reiskind 1969, 1970, 1977; Cushing 1997, 2012). By means of myrmecomorphy, many spiders and insects resemble their models through behavioral and morphological convergence (McIver & Stonedahl 1993; Cushing 1997, 2012; Debandi & Roig-Juñent 1999). Many mimetic spiders have a constricted carapace that gives them a three-segment body appearance, and some have specialized setae on the carapace providing color patterns similar to those on the model ant's gaster. Moreover, numerous myrmecomorphic spiders lift the first pair of legs off the ground and carry out exploratory movements while contacting the substratum much like the antennal movement of ants (antennal illusion), and this behavior further increases the mimetic resemblance (McIver & Stonedahl 1993).

Most ants are unpalatable for generalist predators because they have efficient defense mechanisms, such as hard integument, sometimes with spines, strong mandibles, and stings connected to the poison gland, which expel irritating acid substances. Further, ants can act en masse to attack or defend the colony (Reiskind 1977; Oliveira 1988; Hölldobler & Wilson 1990; Cushing 1997, 2012; Joron 2003). Ants inhabit almost all terrestrial habitats and have few specialized predators. For this reason, ants constitute a stable model for Batesian mimics (Oliveira 1986). Myrmecomorphy is observed in 45 families of insects and in nine families of spiders (McIver & Stonedahl 1993; Cushing 1997).

Over 200 species of ant-mimicking spiders are presently known (Cushing 1997, 2012). The majority is found among salticids (e.g., *Myrmarachne, Synemosyna, Synageles, Belippo, Zuniga*), corinnids (e.g., *Castianeira, Myrmecium, Myrmecotypus, Sphecotypus, Mazax*), gnaphosids (e.g., *Micaria*), thomisids (e.g., *Amyciaea, Aphantochilus*), and zodariids (e.g., *Zodarion, Storena*) (Reiskind 1969, 1977; Foelix 1996; Cushing 1997, 2012; Pekár & Křál 2002). However, studies on

myrmecomorphy of spiders in Argentina are scanty. Galiano's (Galiano 1965, 1966, 1967, 1969, 1996) revisions of the "formiciformes" salticids cite the genera *Sarinda, Martella* and *Synemosyna* for Argentina as imitative species of ants. The purpose of this paper is to present ant mimicry in *Myrmecotypus iguazu* Rubio & Arbino 2009 and to describe the adaptations responsible for the ant-like appearance and behavior in the mimic, with evidence from field and laboratory observations, as well to discuss aspects of spider myrmecomorphy.

Specimens were collected in two localities of the Iguazú and General M. Belgrano Departments, Misiones Province, Argentina: Iguazú National Park (INP – 25.683333°S, 54.433333°W) and Urugua-í Wildlife Reserve (UWR – 25.974345°S, 54.116330°W). The environment consists of subtropical rainforests, which corresponds to the Paranaense phytogeographic region (Cabrera & Willink 1973). The annual temperature and annual precipitation vary between 16 and 22 °C, and 1000 and 2200 mm respectively (Placci & Di Bitetti 2006).

The study was carried out in both the field and laboratory. Spiders and ants were observed, photographed and sampled in January 2005 and January 2009. The specimens were captured during the day, mainly on the handrails of the different tourist circuits of the INP (Fig. 3G). In the laboratory, the experiments were conducted in January 2009 in the CIES (Centro de Investigaciones Ecológicas Subtropicales – INP). The aims of these experiments were 1) to describe the behaviors in the field, 2) to observe the general reactions of the model and mimic toward one another and 3) to test the hypothesis that the myrmecomorphs might be aggressive mimics. Aggressive mimics are species that use deceptive signaling (morphological and/or behavioral) to lure their own prey (Wickler 1968; Vane-Wright 1980). Examples of possible aggressive spider myrmecomorphs include *Aphantochilus* and *Strophius* (Thomisidae) that were observed in same sampling localities carrying ants in their chelicerae (Oliveira & Sazima 1984, 1985). The dead ant carried by the spider is hypothesized to provide chemical cues that serve to lure other ants close to the spider predator.

All experiments were carried out with adult specimens of the myrmecomorphic spider, *Myrmecotypus iguazu* (Corinnidae: Castianeirinae) and the proposed model, *Camponotus sericeiventris* (Formicidae: Formicinae). *Myrmecotypus iguazu* is known from the type
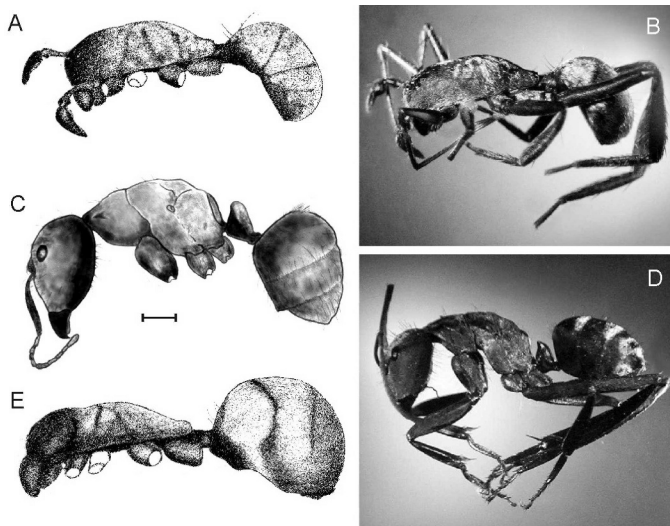
Figure 1.—Close resemblance between the mimetic spider *Myrmecotypus iguazu* (A, B: male; E: female) and its ant worker model *Camponotus sericeiventris* (C, D), lateral view. Note the lengthened carapace with slightly darker coloration in the anterior part simulating the head and thorax of ant, the transverse black bands in the spider's abdomen resembling the segmented gaster of the ant, and the similar pattern of golden reflective pubescence of both species (photos). Scale = 1 mm.

locality in INP and from UWR (Rubio & Arbino 2009). The ant *C. sericeiventris* is exclusively Neotropical and is subdivided into six subspecies (Wheeler 1931; Kempf 1972; ITIS 2013). In Argentina, *C. sericeiventris* is found in Chaco, Corrientes and Misiones provinces (Wheeler 1931; Cuezzo 1998), and according to Wheeler (1931) the subspecies to which we refer is *C. sericeiventris sericeiventris*, although of a slightly smaller size than that of the original description.

To test the hypothesis that *M. iguazu* is an aggressive mimic, one female or one male was placed inside a Petri dish (95 mm diameter) with a moistened piece of filter paper and a twig with leaves that could serve as the spider's retreat. Because there was little difference in size and overall appearance between male and female spiders, we used either one in the experiment. Three minor/median ant workers of *C. sericeiventris* were added to each dish with an adult (female or male) *M. iguazu*, and the behavior of the spider in the presence of multiple models was observed. For each encounter between spiders and ants, three replicates were carried out with observation sessions of 60 min for each one. We used a different set of ants for each trial. Three different females and three different males of *M. iguazu* were used. We performed 18 tests. Interactions between spiders and ants were also observed in the field. If *M. iguazu* is an aggressive mimic, we expected spiders to pursue ants in the Petri dishes. If the spider is a myrmecomorph but not an aggressive mimic, then we expected to see avoidance behaviors on the part of the spiders.

Selection for ant mimicry in spiders influences their behavior, habitat preference and morphology (McIver & Stonedahl 1993). In this analysis, certain morphological indices for mimicry were measured: comparing the values of *M. iguazu* with those of the myrmecomorphic species *Myrmecotypus rettenmeyeri* Unzicker 1965 (see Reiskind 1969), which also mimics the ant *C. sericeiventris*, and with a sympatric non-mimetic corinnid *Falconina gracilis* (Keyserling 1891). Reiskind (1970) indices can be used as indicators of mimicry and are derived by dividing the width by the length of the body segments (see below). Any elongation of structures (carapace, sternum or abdomen) will result in low index values. Ant-mimicking spiders should have low indices, since thinness and elongation of the overall body (cephalothorax and abdomen) often enhance the
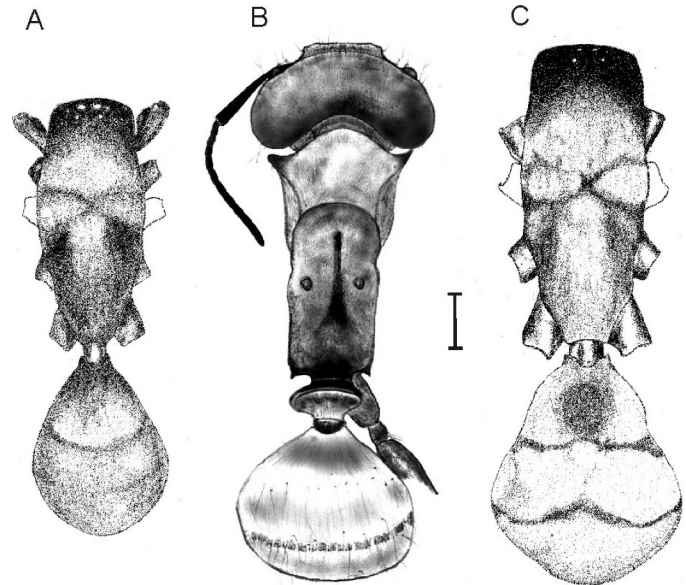

Figure 2.—Dorsal view of the mimetic spider *Myrmecotypus iguazu* (A: male; C: female) and its ant worker model *Camponotus sericeiventris* (B). Note the lengthened carapace with slightly darker coloration in the anterior part simulating the head and thorax of the ant, the transverse black bands in the spider's abdomen resembling the segmented gaster of ant, and the dorsal golden or silver reflective pubescence (whitened area in the drawing) of both species. Scale = 1 mm.

mimetic resemblance. The following indices were used: 1) carapace index = carapace width / carapace length $\times$ 100; 2) sternum index = sternum width / sternum length $\times$ 100 and 3) abdomen index = abdomen width / abdomen length $\times$ 100. The latter index is often particularly important in male myrmecomorphs whose abdomens are completely covered by sclerites, making this index less variable.

We used a Leica® MS5 stereoscopic microscope for photographs. Other photos of ants and spiders in their natural habitat were taken with a Nikon® D80 digital camera. All measurements were taken with a micrometric ocular micrometer and were recorded in millimeters. Voucher specimens of the species examined were deposited in the following institutions: Colección Nacional Aracnológica, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-Ar 19708, 19709); Museo de La Plata (MLP 17926); Colección Aracnológica de la Cátedra de Diversidad Animal I, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba (CDA 000.806 to 000.811); and Colección de Artrópodos de la Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (CARTROUNNE 7818) (see Rubio & Arbino 2009).

Solitary male and female *M. iguazu* were found wandering among workers of *C. sericeiventris* (ratio of 5 spiders to 95 ants in a group of approximately 400 ants). The field observations supported a strong resemblance between the purported mimic and model in morphology, coloration, and behavior. It was very difficult to detect the spiders among the ants (Fig. 3F).

Morphological and coloration convergences.—Ant workers have opaque black bodies that are dimorphic in color, with 80% of individuals covered with a dense pubescence of all golden setae and 20% covered with all silver setae over the alitrunk, petiole, coxae, and gaster (Figs. 1C, D; 2B; 3B, D). This notable golden or silver pubescence is completely reflective. The antennae are long and the third pair of legs longer than the rest (Fig. 3B, D). The workers are polymorphic (Wheeler 1931; Yamamoto & Del-Claro 2008); the
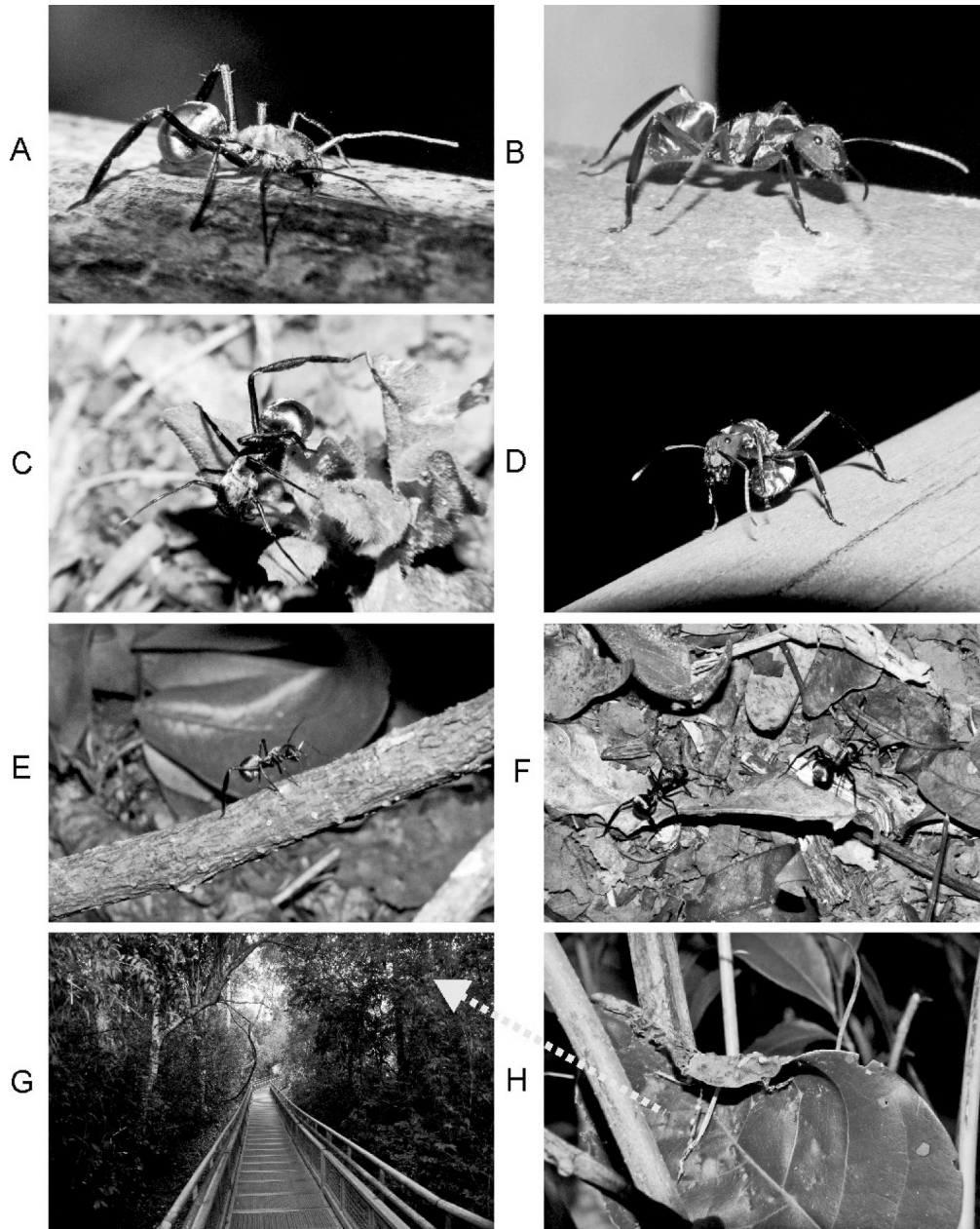
Figure 3.—Habitus and nature of the mimetic spider *Myrmecotypus iguazu* and its ant worker model *Camponotus sericeiventris* in Iguazu National Park, 2009 (A, C, E: female spiders; B, D: ant worker; F: both species wandering in a trail over the ground; G: habitat that the species inhabit; both spiders and ants wander the handrails of the paths together; H: spider refuge in a fold of a green leaf of the foliage, indicated by an arrow.

larger workers vary between 15–16 mm, and median and minor workers between 10–13 mm (Figs. 1C; 2B).

Morphological and color resemblances of female and male *M. iguazu* are evidenced in the lengthened carapace with a sinuous side view and narrow dorsum (Fig. 1A, B, E). A slight constriction in the anterior third, marked with a black line, gives the impression of a division of the cephalothorax into a cephalic region and a separate thoracic region, resulting in the three-segment appearance of body characteristic of ants (Fig. 1E). The head mimicry is emphasized by darker coloration in the anterior third of the carapace and by strong chelicerae resembling ant jaws. The abdomen is oval, with two faint thin transverse black bands shaped by different colors of hair; this aspect looks like the tergites of the ant abdomen (Figs. 1A, E; 2A, C).

In addition, the resemblance is reinforced by the opaque black coloration of the body and by the reflective golden pubescence on the abdomen and posterior region of the carapace (Fig. 3A, C).

The largest females *M. iguazu* reach a total length of 9.7 mm and males 7.3 mm; relative leg lengths longest to shortest are IV-I-III-II, with the first pair much thinner than the others (Rubio & Arbino 2009) (Figs. 1B; 3A, C). Relative leg lengths in *C. sericeiventris* are III-II-I, the third pair corresponding to the fourth pair in spiders. The following morphological indices were mimicry indicators for *M. iguazu* (see Rubio & Arbino 2009), and values in parentheses were given by Reiskind (1969) for *M. rettenmeyeri*: Male: carapace index 43.4 (39); sternum index 46.2 (39); abdomen index 68.9 (66). Female: carapace index 42.1 (38–39); sternum index 37.7 (39–41); abdomen

index 78.7 (69–87). In comparison, the non-mimetic corinnid *Falconina gracilis* had the following indices: male carapace index 74.5, sternum index 87.9, and abdomen index 62.7; and female carapace index 87.2, sternum index 91.7 and abdomen index 62.1. The abdomen indices in *Myrmecotypus* species were high due to the globose abdomens of these mimics.

Behavioral mimicry.—*Myrmecotypus iguazu* wandered actively on the handrails of the paths together with workers of *C. sericeiventris*, moving quickly and stopping sporadically (Fig. 3A, E). The locomotion was always carried out with the first pairs of legs raised forward and moved with slight swinging movements, touching the substratum with the tip of the tarsus, simulating the ants' antennae (Fig. 3A, B, E). Moreover, the tip of the abdomen was slightly curved down, contacting the substratum with the spinnerets, as do ants with the gaster. When perturbed, the spiders adopted a posture comparable to ants facing a similar situation: spiders put the abdomen under the carapace, pointed forward (spray illusion), as the ants do when expelling formic acid (Fig. 3D).

As light levels decreased with approaching night the ants returned to their nests in the rainforest vegetation; the spiders ascended searching a refuge in the foliage, generally in a fold of a green leaf where they weave a retreat as do other corinnids (Fig. 3H). However, during twilight hours one female *M. iguazu* was observed walking alone on the ant trails, although the workers of *C. sericeiventris* had already moved to their nests.

Spiders and ants wandered together in the same places/trails, and encounters between the two seemed to be random. The laboratory experiments resulted in mutual avoidance in all 18 tests with the six spiders; each encounter of a spider with an ant resulted in a quick escape by both model and mimic, especially by the spider, which ran lengths of about 60 mm avoiding contact even before contact occurred. In a typical encounter, the spider walked away from the ant before resuming its movement around the dish. Similar avoidance behavior was observed in the field.

Myrmecotypus rettenmeyeri, a Panamanian spider that resembles *C. sericeiventris,* has this single species as its model (Reiskind 1969). Similarly, *M. iguazu* is an ecological equivalent of *M. rettenmeyeri*, whose males and females are specialized mimics of the same ant species, *C. sericeiventris* (Fig. 3A, B, F).

Support for mimicry.—The following characteristics were considered to demonstrate the existence of mimicry among the species studied (Reiskind 1977): 1) Sympatry: both spiders and ants are found in the same microhabitats of both localities and are found wandering together. 2) Similarity involves morphological and ethological aspects, and patterns of coloration. These aspects were remarkably similar between the species, as was shown in this study. 3) Species specificity: the mimic possesses some structures analogous to the model that are not present in related species of the same genus. The features that fulfill this criterion are the reflective pubescence over the carapace and abdomen of the spiders, and the golden coloration of this pubescence, similar in distribution to the workers of *C. sericeiventris*. However these characteristics are an "indirect proof" of myrmecomorphy according to Reiskind (1977).

Function of mimicry.—Most myrmecomorphic spiders are presumed to be Batesian mimics (Cushing 1997; Oliveira 1986, 1988; McIver & Stonedahl 1993; Reiskind 1977). *Myrmecotypus iguazu* were difficult to differentiate when they moved among the ants because of their morphological and behavioral resemblance to the model ant, even when they wandered separately. Presumably, this protects the spider from ant-averse predators. We propose that the spider *M. iguazu* has evolved as a Batesian mimic of the ant *C. sericeiventris*; however, more work must be done to test this hypothesis. Other studies have supported the hypothesis that myrmecomorphic spiders are Batesian mimics (Engelhardt 1970; Cutler 1991; Nelson & Jackson 2006, 2009; Nelson et al. 2006; Huang et al. 2011; Durkee et al. 2011; Nelson 2012). The behavioral

experiments provided no support for the hypothesis that the spiders are aggressive mimics because they avoided the models in all tests.

In the field samplings, a lizard (*Tupinambis merinae*) was observed removing a prey (Odonata) that was carried by *C. sericeiventris* workers. The lizard stripped the prey of ants with its front legs without ingesting any of these ants and consumed it. This observation suggests that these ants may be unpalatable to at least some arthropod predators, and that the lizards can recognize ants as undesirable.

Camponotus sericeiventris has a wide distribution in tropical America, and considering its size, its dense reflective pubescence and its populous colonies, it is one of the most conspicuous ants of tropical America. For this reason the model is commonly imitated by different arthropod groups. *Eplophorus velutinus* (Coleoptera: Cerambicidae) in Honduras (Wheeler 1931), *Myrmecotypus rettenmeyeri* in Panama (Reiskind 1965) and *Pappognatha myrmiciformis* (Hymenopera: Mutiliidae) in Panama (Wheeler 1983) have been mentioned as mimetic of *C. sericeiventris*.

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